

Leguminosae

Legume family

Peter L. Weaver

Andira inermis (W. Wright) DC., known as cabbage angelin or simply angelin, is an unbuttressed, evergreen tree, with flat, rounded crowns. Mature specimens in Puerto Rico and the West Indies are 15 m tall and 30 cm in diameter at breast height (d.b.h.). In Central and South America, angelin can be 35 m in total height and 1.5 m in d.b.h., with clear boles of 20 m. Leaves are alternate and odd pinnate, with 7 to 25 leaflets. The bark is light gray with a cabbagelike odor. Angelin is adapted to a wide range of sites and produces large crops of seeds. The tree has been used for coffee shade and produces high-grade cabinet wood.

HABITAT

Native Range

Angelin grows in the West Indies from Cuba (48), Jamaica (1), and the Dominican Republic (46), across the Lesser Antilles (5) to Trinidad (4, 36, fig. 1). It is also found from central Mexico (13, 40, 44), Honduras (50), and Costa Rica (24) to Venezuela (41), Peru, Bolivia, and Brazil (30). Moreover, it is native to the Florida Keys and has been introduced to southern Florida. It is also found in eight countries of western tropical Africa (25, 43), where it was introduced from Central America (28).

Angelin was a component of Puerto Rico's original coastal plain and foothill forests, ranging up to about 150 m in elevation (53). Today it is common in all of Puerto Rico except the upper mountains. It occurs in woodlands; along fencerows, river banks, and roadsides; and in pastures. In Guanacaste, Costa Rica, it grows naturally throughout the coastal lowlands and foothills. Deforestation, however, has limited mature trees to gallery forests, pastures, and fencerows (27). In the Dominican Republic, it is very common in woodlands and woodland margins, often in secondary forests (1).

Climate

Angelin is adapted to a variety of frost-free climatic regimes ranging from semihumid through humid to wet. In Puerto Rico, angelin grows in areas where the mean

annual temperatures are 23 to 25 °C (9). Elsewhere in the Caribbean Islands, angelin is found in areas where mean annual temperatures vary from 22 to 26 °C. In continental areas where angelin grows, mean annual temperatures approximate those of the Caribbean.

Mean annual rainfall in Puerto Rico, the remaining Antilles, and Trinidad ranges from 1000 to over 3000 mm/yr. In Costa Rica, angelin was recorded in wet forests where mean annual rainfall is 4000 mm/yr. Specific years had rainfall of 2900 and 5600 mm/yr (19). It was also found in Costa Rican dry forests where mean annual rainfall is 1530 mm/yr, with extremes of 1000 and 2260 mm/yr. In the dry forests of Colombia and Venezuela where angelin grows, mean annual rainfall varies between 1000 and 1800 mm/yr (15, 16).



Figure 1.—Range of cabbage angelin (*Andira inermis*) in the tropics.

Peter L. Weaver is research forester, Institute of Tropical Forestry, Southern Forest Experiment Station, USDA Forest Service, Rio Piedras, PR, in cooperation with the University of Puerto Rico, Rio Piedras, PR.

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Soils and Topography

Angelin grows on a variety of soils. In Mexico, it is found on sandy soils as well as on poorly drained clays (40). In Cuba, it was observed on the south coast in deep valleys without seaward exposure and at elevations ranging from sea level to nearly 1000 m (48). On the relatively dry island of St. John, the U.S. Virgin Islands, angelin was found in moist gullies from near sea level to 330 m in elevation (59). In the Guianas, it generally grows in swamps and marsh forests (32).

Associated Forest Cover

Because angelin is adapted to a variety of sites, it grows in several forest types with numerous tree species throughout its range (table 1). In the Lesser Antilles, angelin was recorded in seasonal and dry evergreen forests (5). In Nicaragua, it was found in lowland evergreen rain forests (51), and in Costa Rica, in tropical dry, tropical moist, tropical wet, and premontane moist forests (20, 23, 45). Angelin was also found in the tropical dry forests of Colombia and Venezuela (15, 16).

In Puerto Rico, angelin is a common component of most secondary forests, ranking fourth in total basal area (6). It grows mainly in the subtropical wet and moist forests (17), but also has been recorded in subtropical dry forests (30). At lower elevations in the Luquillo Mountains of Puerto Rico, angelin is relatively uncommon (49, 54), ranking 28th in the stem density and 25th in both basal area and volume for all trees sampled on 4 ha of permanent plots (7). In the wet forest of Corcovado National Park, Costa Rica, it was also reported as relatively uncommon, averaging only 2.3 mature individuals per hectare (22).

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting.—The pink to purple pea-shaped flowers of angelin, each about 2 cm long and lasting just 1 day, are produced in terminal panicles and appear from February through April in the Guanacaste area of Costa Rica (26, 27). Flowering synchronization occurs among members of a population. Each tree blooms for about 20 days, and flowering lasts for about 30 days within a single population, (20). In the wet Golfo Dulce area of Costa Rica, differences in flowering by tree size were apparent. Mature trees flowered once during March and April; smaller trees flowered twice, first in March and April and again in July and August during the shorter dry season (2). In comparative phenological studies between wet and dry forests of Costa Rica, angelin had no significant period of leaf fall in the wet forest, a discontinuous production of new leaves between January and June, and a March flowering period (19). This contrasted with the dry forest, where leaf drop and leaf flushing were concentrated in November, and flowering was mainly in Febru-

ary (19). In Trinidad, flowering was observed in April and October (37).

The fruits are egg-shaped, 2.5- to 4-cm long green pods that contain a single poisonous seed (30). In Costa Rica, fruits ripen from mid-May to late June. The seeds are surrounded by a thick, fibrous husk, with a thin layer of juicy, white pulp between the husk and the epidermis of the fruit.

Four families, 9 genera, and 70 species of bees were identified on angelin flowers (20). Although they moved infrequently between conspecific trees, this movement was judged sufficient to effect pollination and result in fruit set. Studies of controlled pollination on five trees indicated that fruit set was much higher in cross-pollinated flowers than in open-pollinated flowers. Self-pollinated flowers produced a few fruits, but all dropped when small, demonstrating that the species is self-incompatible.

Seed Production and Dissemination.—Angelin produces large seed crops. In a 2.3-kg sample used to determine fruit weights, fruits averaged 30 per kilogram when wet and 50 per kilogram when dry. Moisture contents of the same sample were 53 percent for wet fruit and 26 percent for dry fruit. A cutting test of 25 fruits showed that all contained seeds.

In Trinidad, seed dispersal was primarily by bats (37). Natural regeneration was not considered good, however, because seedlings did not seem to develop. In Costa Rica, bats were identified as the principal consumers and dispersers of angelin fruits (21, 27). *Aratinga* parrots were also observed feeding on the pulp. Once fruits were on the ground, small rodents, leaf-cutting ants, and other miscellaneous insects ate the pulp.

Seedling Development.—Germination is hypogeous (37). Tests in Puerto Rico showed 100-percent germination for 20 seeds sown immediately after collection. For 20 seeds stored in bags at room temperature and sown after 6 weeks, germination was 80 percent. In a nursery trial, 100 seeds were sown on plots in full sunlight and 100 seeds were sown on plots under shade. After 3, 4, and 5 months, the plots in full sunlight had produced 36, 40, and 49 seedlings with heights of 18, 28, and 32 cm, respectively. Plots in shade produced 13, 17, and 33 seedlings for the same time intervals, with respective heights of 13, 28, and 36 cm.

Germination of angelin in Puerto Rico was listed as fairly good by Marrero (33). In a direct seeding experiment in the moist limestone forest at Cambalache, 100 seed spots of angelin, each containing 2 seeds, were established under partial shade. The site was weeded when necessary, and the overstory was opened. After 5 years, heights ranged from 0.6 to 1.2 m. After 10 years, height averaged 1 m, with a maximum height of 1.5 m. Growth was exceptionally slow, the form shrubby, and seedlings on poor sites were chlorotic. Because of these poor results, angelin was not considered for reforestation in Puerto Rico after 1950 (34). Similar findings were reported for Trinidad, where seedlings persisted after transplanting but did not grow well (37).

In the wet forests of Corcovado, Costa Rica, it appeared that angelin sapling mortality was greater than seedling mortality (22). It was suggested that this failure of a substantial portion of the sapling population to survive to

Table 1.—Major tree species associated with cabbage Angelin (*Andira inermis*)

Country	Locailty	Elevation	Rainfall	Principle associated species ¹	Source
		<i>m</i>	<i>mm/yr</i>		
Colombia	Tropical dry forests	0-1100	1000-2000	<i>Ceiba pentandra</i> <i>Anacardium excelsum</i> <i>Spondias mombin</i>	(15)
Costa Rica	Evergreen lowland rain forest	flood plains	2500-5000	<i>Anacardium excelsum</i> <i>Brosimum</i> spp. <i>Cedrela mexicana</i>	(2)
	Lower montane rain forests	<600	>4000	<i>Brosimum utile</i> <i>Coccoloba roseiflora</i> <i>Vochysia</i> spp. Nine other associations with numerous species	(2)
	Tropical dry forests	0-70	1000-2000	<i>Anacardium excelsum</i> <i>Tabebuia pentaphylla</i> <i>Pithecolobium dulce</i>	(23, 45)
	Tropical moist forests	35	2000-4000	<i>Enterolobium cyclocarpum</i> <i>Pithecolobium saman</i> <i>Spondias mombin</i>	(23, 45)
	Tropical wet forest	140	>4000	<i>Brosimum utile</i> <i>Calophyllum brasiliense</i> <i>Hymenaea coubaril</i>	(23, 45)
Cuba	Pico Turquino	150-750	 ²	<i>Calophyllum antillanum</i> <i>Cordia alliodora</i> <i>Tabebuia pentaphylla</i>	(47)
	South coast, deep valleys near coast	<150		<i>Guarea guidonia</i> <i>Mastichodendron foetidissimum</i> <i>Petitia dominguensis</i>	(48)
	South coast, Monte Fresco	0-500		<i>Cedrela mexicana</i> <i>Calophyllum candidissimum</i> <i>Swietenia mahagoni</i>	(48)
	North and South slopes	150-900		<i>Cedrela mexicana</i> <i>Guarea guidonia</i> <i>Prunus occidentalis</i>	(48)
	Sierra de Nipe	0-1000	1000-1500	<i>Nectandra coriaceae</i> <i>Calophyllum antillanum</i> <i>Guarea trichiloides</i>	(10)
Lesser Antilles	Several Islands	<200	2000	<i>Nectandra coriaceae</i> <i>Terminalia catappa</i> <i>Bursera simaruba</i>	(5)
Mexico	Chiapas	200-600	1700-1900	<i>Calophyllum brasiliense</i> <i>Licania sparsipilis</i> <i>Ceiba pentandra</i> on inundated areas	(44)
				<i>Hymenaea coubaril</i> <i>Nectandra globosa</i> <i>Ficus glabrata</i> on deep soils near rivers	(44)
Nicaragua	Lowland			<i>Carapa nicaraguensis</i>	(51)

Table 1.—Major tree species associated with cabbage Angelin (*Andira inermis*)—Continued

Country	Locality	Elevation	Rainfall	Principle associated species ¹	Source
		m	mm/yr		
	evergreen rain forest			<i>Dipteryx panamensis</i> <i>Terminalia amazonia</i>	
Puerto Rico	Luquillo Mountains	150-500	3000+	<i>Dacryodes excelsa</i> <i>Sloanea berteriana</i> <i>Manilkara bidentata</i>	(7)
	Secondary forest	0-400	1500-2000	<i>Inga vera</i> <i>Guarea guidonia</i> <i>Cecropia peltata</i>	(6)
Trinidad	Evergreen seasonal forest	0-250	1800-3000	<i>Carapa guianensis</i> <i>Eschweilera subglandulosa</i> association: ranked from 8th to 28th in stem density in 6 faciations as emergent tree	(4)
	Semi-evergreen forest	Lower slopes	<1500	<i>Peltogyne porphyrocardia</i> association: ranked from 15th to 38th in stem density in 4 faciations as upper story tree	(4)
	Deciduous seasonal forest	Mountainous	1100-1500	<i>Bursera simaruba</i> <i>Lonchocarpus punctatus</i> association: ranked 18th in stem density in 1 faciation as emergent tree	(4)
	Seasonal montane forests	>500	high rainfall, misty	<i>Inga macrophylla</i> - <i>Guarea guara</i> association: ranked 36th in stem density as a lower story tree	(4)
Venezuela	Tropical dry forests	400-1000	1000-2000	<i>Spondias mombin</i> <i>Tabebuia</i> spp. <i>Cassia</i> spp.	(16)

¹Only a few associated species have been listed for each site; most species lists from the cited references are extensive.

²Information not given in columns or rows is not available.

maturity could be attributed to the loss of vigor and resistance associated with the attainment of reproductive maturity. Understory trees characteristically produce large inflorescences at an early age.

Vegetative Reproduction.—Angelin coppices fairly well but does not produce root suckers (37).

Sapling and Pole Stage to Maturity

Growth and Yield.—Information on the growth of angelin is scarce. After 9 years, seedlings planted in Puerto Rico had a mean height growth of only 0.2 m/yr and a mean diameter growth of 0.28 cm/yr (table 2). In secondary forests, diameter growth ranged between 0.10 and 0.16 cm/yr. None of the crown classes showed rapid incre-

ment. In Trinidad, angelin was reported as slow growing in early stages, averaging about 0.8 m/yr during the first 3 years (37).

Rooting Habit.—Angelin is moderately deep rooted (37). In a survey of root systems in the tabonuco forest of Puerto Rico, angelin was found to have large nodules (14). Because the species is leguminous, it was assumed that the nodules served in a nitrogen-fixing capacity.

Reaction to Competition.—Angelin is moderately shade tolerant (40). It requires shade for germination, and although it is tolerant of shade while growing, it develops better where gaps exist in the forest canopy (22). In Trinidad, where detailed work was done on tree distributions in several different forest types, angelin was ranked as a relatively uncommon tree (4). Moreover, the species

Table 2.—Growth information for cabbage angelin (*Andira inermis*)

Country	Locality	Elevation	Rainfall	Survival	Duration	Mean growth		Comments	Source
						Height	D.b.h.		
		<i>m</i>	<i>mm/yr</i>	<i>Percent</i>	<i>Yrs</i>	<i>m/yr</i>	<i>cm/yr</i>		
Puerto Rico	Guajataca	300	1900	Fair	9	0.2	0.28	Trees planted on lower slope terrain in limestone hills	(34)
Puerto Rico	Secondary forests	0–600	1000–2000	 ¹	5		0.16	The d.b.h. increments in cm/yr by crown class for 43 trees in moist and wet secondary forests were: 0.11 for dominants, 0.18 for codominants, 0.18 for intermediates, and 0.15 for small trees not classified	(58)
Puerto Rico	Secondary forests	40	1900		32		0.10	For three 5- to 8-cm d.b.h. trees in a woodlot	(60)

¹Information not given in columns or rows is not available.

was recorded as an emergent in seven faciations of two associations, as an upper story tree in four faciations of another association, and as a lower story tree in yet another association (table 1). In Costa Rica, it was recorded in the upper canopy in seasonally wet forests, whereas in perennially wet forests it was an understory species (22). Angelin also reaches the canopy in both Puerto Rico's secondary forests and, occasionally, in the undisturbed wet forests of the Luquillo Mountains.

Angelin has been used for coffee shade in Puerto Rico (6, 35). Given its value as a timber species, thinnings were suggested as a means to improve its growth potential and that of other timber species found in abandoned coffee plantations (57).

Damaging Agents.—The sapwood portions of angelin logs are highly susceptible to discoloration by sap-staining fungi. The sapwood is also subject to attack by pin-hole borers and powder-post beetles and is not resistant to termites (11, 29, 31, 32). The heartwood is resistant to attack by decay fungi and insects but only moderately resistant to dry-wood termites (8, 11, 31, 39, 62).

In Costa Rica, angelin wood was reported as durable, resistant to decay when in contact with the ground or in water, resistant to insect attack (2), and moderately resistant to marine borers (31). However, predation by *Cleogonus* spp. seed weevils was observed, particularly below parent trees (27). In Trinidad, angelin was reported free of major diseases although seeds were often bored into by a fruit fly (37). Field mice clipped the stems of many seedlings in Puerto Rico (30).

Angelin has been damaged by hurricanes in Puerto Rico. Hurricane San Felipe of 1928, a very destructive storm, caused defoliation, crown breakage, and splitting of trunks in different areas of the island (3). Angelin, however, proved wind resistant to hurricane Santa Clara, a comparatively mild storm, which passed over Puerto Rico in 1956 (56).

Special Uses

Angelin is hard, heavy (specific gravity of 0.64 g/cm³), rather coarse grained, tough, and strong (2, 41). The wood seasons at a moderate rate without serious degrade and can be worked easily with both hand and machine tools (31). Alternate bands of dark and light fibers give the wood an attractive appearance but make it difficult to plane to a smooth surface (11, 32). Nails enter the wood easily, and the wood glues satisfactorily and finishes well, but it lacks luster.

In the American tropics, angelin is used for high-grade furniture and cabinetwork because of its grain and attractive coloration. Other uses include turnery, billiard cue butts, and logging cart wheels; pilings, railroad ties, bridge timbers, and other heavy construction (2); umbrella handles and canes; carpentry, vehicles, and boats (30); decorative veneer; and parquet flooring (11). Because the wood has virtually no resonance, it is particularly suitable for radio and television cabinets (31).

In Puerto Rico, angelin was formerly used for furniture and cabinetwork, but when larger sized trees were no longer available, it was used for fenceposts and poles (30, 55). In a study to determine the penetration of preservatives to improve the durability of posts, angelin stems 1.3 m long by 8 cm in diameter were soaked for 120 hours in a 5-percent solution of pentachlorophenol in diesel oil (52). Results showed that the stems absorbed 0.36 kg/m³ of solution.

Angelin was recommended for ornamental planting because of its attractive flowers (61). Moreover, it has been suggested as shade for coffee where it can also provide timber for rural populations (38).

The bark has been used as a vermifuge, purgative, and narcotic, but in large doses it is a dangerous poison (12). The seeds contain a poisonous alkaloid (2, 43, 50). The plant has also been implicated in the sudden death of cat-

tle in Cuba (18). Smoke from the wood is reported to be injurious to the eyes (30).

GENETICS

Allen (2) felt that the genus *Andira* needed to be revised and noted that possibly two species were present in the Golfo Dulce of Costa Rica. He observed that some of the smaller trees had much larger panicles of darker flowers than the larger trees, and he observed that the smaller trees also had two flowering seasons whereas larger trees bloomed only once during the year. These characteristics, however, could be attributed to differences in size. Given the variety of habitats and considerable range of angelin, it is possible that varieties and even different species exist.

Angelin was previously named *A. jamaicensis* (W. Wright) Urban, *Geoffroya inermis* W. Wright (30), and *Lonchocarpus staudii* Harms (25). A closely related species, *A. racemosa*, is reported from Martinique and Guadeloupe (32).

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